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## CAROTENOIDS AND SEXUAL DICHROMATISM IN NORTH AMERICAN PASSERINE BIRDS

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**Abstract.**—Sexual dichromatism and the extent of male carotenoid-derived plumage coloration in breeding season North American passerine birds was analyzed by phylogenetic statistical methods. Passerines as a whole and five passerine subclades were analyzed by both independent contrasts and simulation methods. In passerines as a whole, carotenoids and sexual dichromatism are positively correlated irrespective of analysis method. In three of the subclades, the correlations are significant by a clear majority of analysis methods. Neither melanin nor structurally derived colors show similar significant increases with dichromatism. Carotenoids are obtained by animals solely through the diet, whereas both melanins and structurally derived colors can be synthesized. The relationship between sexual dichromatism and the use of carotenoids in plumage suggests that sexual selection may have promoted the expression of a condition-dependent honest indicator of phenotypic quality.

In birds with nuptial display feathers, carotenoids undoubtedly play a positive rôle which is possibly a true sexual function. (GOODWIN 1952, p. 267)

The function(s) of sexual dichromatism and bright plumage coloration has been the focus of much research and debate (Darwin 1871; Sibley 1957; Selander 1972; Baker and Parker 1979; Hamilton and Zuk 1982). Largely missing from this debate has been a consideration of the biochemical basis of plumage coloration. The majority of avian plumage coloration is produced by one, or a combination of several, of four major types of color determinants. Three of these four are pigments, namely carotenoids, melanins, and porphyrins; the fourth is due to the physical scattering of light by microscopic airspaces within the keratin of the feather itself and by reflection from the feather barbules—so-called structural coloration (Fox 1976; Brush 1978). In general, white, blue, and iridescent plumage coloration is produced structurally (Fox 1976; Brush 1978); bright red, orange, and yellow plumage coloration is due to carotenoid pigments (Fox and Vevers 1960; Fox 1976; Brush 1978; Hudon and Brush 1992); brown, black, gray, buff, and dull brownish red, dull orange, and dull yellowish plumage coloration is due to melanin pigments (Fox 1976; Brush 1978). Porphyrins produce colors ranging from brown to blue, green, and red. Although widely distributed among avian taxa, porphyrins tend to be restricted to feathers or parts of feathers not exposed

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to direct sunlight (Brush 1978), for example, feather shafts of young pigeons (Fox 1976). Exceptions are owls (Strigidae), bustards (Otididae), and turacos (Musophagidae). As the present analysis is restricted to passerines, and porphyrins tend to be restricted to unexposed feather areas, porphyrins are not considered further here.

Carotenoids are synthesized only in plants, algae, and some bacteria and fungi. Although many animals can modify the structure of ingested carotenoids, no animals have been shown to synthesize them (Fox and Vevers 1960; Fox 1976, 1979; Brush 1978); therefore, all carotenoids found within animals must have been obtained through the diet. Because of this, a condition-dependent signaling role for carotenoids has been suggested by several authors (Kodric-Brown and Brown 1984; Andersson 1986; Hill 1990; Zuk 1992). Melanins are produced in animals by the catabolism of the amino acids tyrosine, tryptophan, and phenylalanine (Fox 1976; Brush 1978). Anabolic and catabolic pathways can interconvert proteins and these amino acids (Fox 1976). For this reason, melanins are less likely than carotenoids to be limited, honest indicators of phenotypic quality. Structural colors are produced by properties of the feather, as previously noted. Feather structure abnormalities are infrequent and usually lethal in wild birds (Harrison 1985). For this reason, structural colors, in and of themselves, are less likely than carotenoid-derived colors to honestly indicate phenotypic quality, except perhaps extreme (i.e., usually fatal) nutritional, disease, or genetic stress.

The basis of avian plumage coloration suggests that carotenoid-derived colors, in and of themselves, have the potential to honestly reflect phenotypic quality, whereas melanin and structurally derived coloration may do so if coupled with an additional honesty-enforcing mechanism. This is not to argue that traits that are synthesized endogenously are necessarily poor indicators of phenotypic quality. What is being argued, however, is that carotenoid pigments by their nature have greater potential to be honest indicators of phenotypic quality than do either melanins or structural colors in the absence of additional honesty-enforcing mechanisms. Clearly many synthesized traits do reflect phenotypic quality, for example, the tail of the male peafowl, *Pavo cristatus* (Petrie 1994), the size of the comb of red jungle fowl, *Gallus gallus* (Ligon et al. 1990; Zuk et al. 1990a), and the size and symmetry of several feather ornaments (Møller and Pomiankowski 1993). Synthesized traits that do honestly reflect phenotypic quality, however, most likely will require an additional mechanism to enforce honesty, for example, strong opposing natural selection, that is, handicap traits (Zahavi 1975, 1991), or testosterone-mediated expression (Folstad and Karter 1992). For example, the badge of the male house sparrow, *Passer domesticus*, is produced by melanin. It acts as a signal of social dominance and status (Møller 1987a). However, so far as anyone knows, the honesty of the badge as a signal is unrelated to the fact that it is produced by melanin. Instead, honesty is maintained through social interaction (Møller 1987b). Testosterone-mediated trait expression seems an unlikely honesty-enforcing mechanism for avian plumage, as male-type plumage in most species of birds develops from the absence of estrogen rather than the presence of testosterone (see Owens and Short 1995).

If sexual selection, either by male-male competition or by female choice, operates on the basis of condition-dependent honest indicators of quality (Zahavi 1975, 1991; Andersson 1982, 1986; Kodric-Brown and Brown 1984; Grafen 1990), then carotenoid, but not necessarily melanin or structural, coloration would be expected to increase in lineages with increased sexual selection. To test this hypothesis, I looked for interspecific correlations between sexual dichromatism and the proportion of carotenoid, melanin, and structurally derived plumage coloration. Specifically, the hypothesis predicts positive correlations between carotenoid-derived plumage coloration and sexual dichromatism.

This argument assumes that sexual dichromatism reflects the accumulated effects of sexual selection rather than other selective pressures (Darwin 1871; Selander 1972; Baker and Parker 1979; Møller and Birkhead 1994). It is also assumed that the biochemical origin of plumage colors can reliably be inferred from the color itself without requiring direct biochemical evidence for all species. This assumption may seem tenuous at best; however, Hudon and Brush (1992, p. 319) state, "Carotenoids produce the majority of bright yellow, orange, and red hues found in birds . . . plumage color is a good indicator of the kinds of carotenoids deposited." That is, not only can the presence of carotenoids reliably be inferred from plumage color, but the specific types of carotenoids may also be inferred. Known exceptions include hummingbird (Trochilidae) gorgets, which are produced structurally, parrot (Psittaciiformes) red and yellow feathers, which have an unknown, but probably noncarotenoid, color origin (Hudon and Brush 1992), and the green and red pigments of turacos (Musophagidae), which derive from the porphyrins turacoverdin and turacin (Fox 1976).

An important difference between this study and previous studies of the evolutionary significance of avian coloration is the analysis of dichromatism and the underlying biochemical nature of coloration. This approach has at least two major advantages. First the concepts of "conspicuousness" and "brightness" are avoided. This is a significant improvement over previous analyses because conspicuousness and brightness are subjective and dependent on ecologically relevant environmental conditions. In addition, as humans almost universally perceive carotenoid coloration as bright, correlating carotenoid coloration with "brightness" would be tautological. Second, the results are more likely to be independent of differences between human and avian sensory systems, which are greater than previously appreciated (Bennett et al. 1994).

## METHODS

### *Data Collection*

North American passerines for which information was available in a standard field guide (National Geographic Society 1987) and in a technical bird-banding guide (Pyle et al. 1987) and for which phylogenetic information was available in Sibley and Ahlquist (1990) were used. Each of 12 plumage regions was scored for sexual dichromatism (i.e., dichromatic or not dichromatic) and probable color origin (i.e., carotenoid, melanin, structural, or a combination of these). Green

coloration can be produced in several ways (Fox and Vevers 1960; Brush 1978), and scoring its color origin is more ambiguous than is scoring red or black. To be conservative when assigning a carotenoid origin to coloration, noniridescent bright green was scored as carotenoid/structural, that is, yellow plus blue (e.g., green jay, *Cyanocorax yncas*; painted bunting, *Passerina ciris*), whereas iridescent green (e.g., European starling, *Sturnus vulgaris*; violet-green swallow, *Tachycineta thalassina*), dull green (e.g., green-tailed towhee, *Pipilo chlorurus*), and olive (e.g., Wilson's warbler, *Wilsonia pusilla*) were scored as melanin/structural. (Note that because of a lack of phylogenetic information, not all of the above examples were used in the analysis.) The plumage regions scored were as follows: crown, eye stripe, auricular, throat, nape, mantle, wing, breast, belly, rump, undertail coverts, and tail. The dichromatism, carotenoid, melanin, and structural scores for the 12 regions were individually summed, averaged within genera, and converted to proportions. The arcsines of the square roots of the proportions were used in analysis. The untransformed generic averages and species values are given in table 1.

### Analysis

Because phylogenetic history will usually cause more closely related species to be more similar than are more distantly related species, species (or even higher taxonomic units) cannot be considered statistically independent data points (Harvey and Pagel 1991; Miles and Dunham 1993). Because of the effects of phylogenetic history, I used a current hypothesis about the phylogeny of passerines (Sibley and Ahlquist 1990) and phylogenetically appropriate analyses. One approach is to compute phylogenetically independent contrasts (Felsenstein 1985, 1988; Harvey and Pagel 1991; Garland et al. 1992). The other is to use simulations to create null distributions for hypothesis testing (Martins and Garland 1991; Garland et al. 1993). These are described separately below.

I used the PDTREE module of the Phenotypic Diversity Analysis Program (Garland et al. 1993; T. Garland, Jr., personal communication) to compute independent contrasts and check that they were adequately standardized (Garland et al. 1992). Contrasts are standardized by dividing them by the square root of the sum of their branch lengths. If a plot of the absolute values of the contrasts versus their standard deviations shows any linear or nonlinear trends, then the contrasts do not receive equal weight in subsequent correlation or regression analyses. When this was the case, the branch lengths were transformed (see Garland et al. 1992). Once contrasts were adequately standardized, they were used for correlation through the origin (Harvey and Pagel 1991; Garland et al. 1992). The correlation was tested for significance against normal statistical tables (e.g., Rohlf and Sokal 1981). Polytomies can reduce the degrees of freedom available for statistical testing (Purvis and Garland 1993). The phylogeny I used contains four polytomies, two in the Tyrannidae and two in the Corvoidea. Because of this, I report statistical significance for the range of minimum to maximum degrees of freedom.

The simulation analyses consist of comparing the observed Pearson correlation across tip values with 1,000 correlations across tip values of data simulated under

TABLE 1

THE SAMPLE OF NORTH AMERICAN PASSERINES USED IN THIS STUDY

ANALYSIS GROUP	GENERIC AVERAGES AND SPECIES VALUES			
	Dichromatism	Carotenoid	Melanin	Structural
Corvoidea:				
<i>Aphelocoma</i> (2)	0	0	5.5	6.5
<i>A. coerulescens</i>	0	0	6	6
<i>A. ultramarina</i>	0	0	5	7
<i>Corvus</i> (5)	0	0	12	0
<i>C. brachyrhynchos</i>	0	0	12	0
<i>C. caurinus</i>	0	0	12	0
<i>C. corax</i>	0	0	12	0
<i>C. cryptoleucus</i>	0	0	12	0
<i>C. ossifragus</i>	0	0	12	0
<i>Cyanocitta</i> (2)	0	0	4	8
<i>C. cristata</i>	0	0	3	9
<i>C. stelleri</i>	0	0	5	7
<i>Cyanocorax</i> (1)	0	3.5	2	6.5
<i>C. yncas</i>	0	3.5	2	6.5
<i>Gymnorhinus</i> (1)	0	0	1	11
<i>G. cyanocephalus</i>	0	0	1	11
<i>Lanius</i> (2)	0	0	7.5	4.5
<i>L. excubitor</i>	0	0	7.5	4.5
<i>L. ludovicianus</i>	0	0	7.5	4.5
<i>Nucifraga</i> (1)	0	0	10	2
<i>N. columbiana</i>	0	0	10	2
<i>Perisoreus</i> (1)	0	0	7	5
<i>P. canadensis</i>	0	0	7	5
<i>Pica</i> (2)	0	0	8	4
<i>P. nuttalli</i>	0	0	8	4
<i>P. pica</i>	0	0	8	4
<i>Vireo</i> (14)	.29	.68	7.18	4.14
<i>V. altiloquus</i>	0	0	8.5	3.5
<i>V. atricapillus</i>	4	.5	5.5	6
<i>V. bellii bellii</i>	0	0	8	4
<i>V. bellii</i> (western forms)	0	0	8	4
<i>V. flavifrons</i>	0	3	5	4
<i>V. gilvus</i>	0	0	7	5
<i>V. griseus</i>	0	2	8	2
<i>V. huttoni</i>	0	0	7.5	4.5
<i>V. olivaceus olivaceus</i>	0	0	7	5
<i>V. olivaceus flavoviridis</i>	0	2	5	5
<i>V. philadelphicus</i>	0	1	7	4
<i>V. solitarius</i> (eastern forms)	0	1	6	5
<i>V. solitarius plumbeus</i>	0	0	9	3
<i>V. vicinior</i>	0	0	9	3
Muscicapoidae:				
<i>Bombycilla</i> (2)	2.5	1.25	10.25	.5
<i>B. cedrorum</i>	3	1.75	9.25	1
<i>B. garrulus</i>	2	.75	11.25	0
<i>Catharus</i> (4)	0	0	9.25	2.75
<i>C. fuscescens</i>	0	0	10	2
<i>C. guttatus</i>	0	0	9	3
<i>C. minimus</i>	0	0	9	3
<i>C. ustulatus</i>	0	0	9	3
<i>Cinclus</i> (1)	0	0	12	0
<i>C. mexicanus</i>	0	0	12	0

TABLE 1 (Continued)

ANALYSIS GROUP	GENERIC AVERAGES AND SPECIES VALUES			
	Dichromatism	Carotenoid	Melanin	Structural
<i>Dumetella</i> (1)	0	0	12	0
<i>D. carolinensis</i>	0	0	12	0
<i>Hylocichla</i> (1)	0	0	9	3
<i>H. mustelina</i>	0	0	9	3
<i>Mimus</i> (1)	0	0	10	2
<i>M. polyglottos</i>	0	0	10	2
<i>Myadestes</i> (1)	0	0	12	0
<i>M. townsendi</i>	0	0	12	0
<i>Oreoscoptes</i> (1)	0	0	10	2
<i>O. montanus</i>	0	0	10	2
<i>Phainopepla</i> (1)	12	0	12	0
<i>P. nitens</i>	12	0	12	0
<i>Sialia</i> (3)	11.33	0	1.33	10.67
<i>S. currucoides</i>	12	0	0	12
<i>S. mexicana</i>	11	0	1.5	10.5
<i>S. sialis</i>	11	0	2.5	9.5
<i>Sturnus</i> (1)	1	0	6	6
<i>S. vulgaris</i>	1	0	6	6
<i>Toxostoma</i> (7)	0	0	10.5	1.5
<i>T. bendirei</i>	0	0	10.5	1.5
<i>T. crissale</i>	0	0	11	1
<i>T. curvirostre</i>	0	0	10	2
<i>T. lecontei</i>	0	0	11	1
<i>T. longirostre</i>	0	0	10	2
<i>T. redivivum</i>	0	0	11	1
<i>T. rufum</i>	0	0	10	2
<i>Turdus</i> (1)	5	0	10.5	1.5
<i>T. migratorius</i>	5	0	10.5	1.5
Passeroidea:				
<i>Agelaius</i> (2)	12	.5	11.5	0
<i>A. phoeniceus</i>	12	.5	11.5	0
<i>A. tricolor</i>	12	.5	11.5	0
<i>Cardinalis</i> (2)	10	6.13	5.38	.5
<i>C. cardinalis</i>	12	8	4	0
<i>C. sinuatus</i>	8	4.25	6.75	1
<i>Carduelis</i> (7)	6.14	3.46	6.82	1.71
<i>C. flammea</i>	2	2	7.5	2.5
<i>C. hornemanni</i>	2	2	7	3
<i>C. lawrencei</i>	8	3.5	7.5	1
<i>C. pinus</i>	2	.75	9.25	2
<i>C. psaltria</i> (black-backed)	10	4	8	0
<i>C. psaltria</i> (green-backed)	9	5.5	5	1.5
<i>C. tristis</i>	10	6.5	3.5	2
<i>Carpodacus</i> (3)	5.67	4.33	6.17	1.5
<i>C. cassinii</i>	4	2.5	7.5	2
<i>C. mexicanus</i>	5	4.5	6.5	1
<i>C. purpureus</i>	8	6	4.5	1.5
<i>Chondestes</i> (1)	0	0	7.25	4.75
<i>C. grammacus</i>	0	0	7.25	4.75
<i>Dendroica</i> (23)	4.39	2.47	6.41	3.12
<i>D. caerulescens</i>	12	0	2	10
<i>D. castanea</i>	8	0	12	0
<i>D. cerulea</i>	10	0	0	12
<i>D. chrysoparia</i>	4	2	7.5	2.5

TABLE 1 (Continued)

ANALYSIS GROUP	GENERIC AVERAGES AND SPECIES VALUES			
	Dichromatism	Carotenoid	Melanin	Structural
<i>D. coronata auduboni</i>	6	3	7	2
<i>D. coronata coronata</i>	5	1.5	6.5	4
<i>D. discolor</i>	3	3.5	6	2.5
<i>D. dominica</i>	3	1.5	7	3.5
<i>D. fusca</i>	7	4	7	1
<i>D. graciae</i>	2	3	7	2
<i>D. kirtlandii</i>	3	2	9	1
<i>D. magnolia</i>	5	3.5	6	2.5
<i>D. nigrescens</i>	4	.25	8	3.75
<i>D. occidentalis</i>	1	2.5	6.5	3
<i>D. palmarum hypochrysea</i>	0	4.5	7.5	0
<i>D. palmarum palmarum</i>	0	3	7.5	1.5
<i>D. pensylvanica</i>	4	1	6.5	4.5
<i>D. petechia</i>	7	11	1	0
<i>D. pinus</i>	4	2	5.5	4.5
<i>D. striata</i>	5	0	9	3
<i>D. tigrina</i>	5	4.5	6	1.5
<i>D. townsendi</i>	1	2.5	7	2.5
<i>D. virens</i>	2	1.5	6	4.5
<i>Dolichonyx</i> (1)	12	0	10.5	1.5
<i>D. oryzivorus</i>	12	0	10.5	1.5
<i>Eremophila</i> (1)	4	3	7.5	1.5
<i>E. alpestris</i>	4	3	7.5	1.5
<i>Helmitheros</i> (1)	0	0	11	1
<i>H. vermivorus</i>	0	0	11	1
<i>Icteria</i> (1)	1	2	7	3
<i>I. virens</i>	1	2	7	3
<i>Icterus</i> (7)	10.29	4.68	7.14	.18
<i>I. cucullatus</i>	12	7	5	0
<i>I. galbula galbula</i>	12	3.75	7.5	.75
<i>I. galbula bullockii</i>	12	6	5.5	.5
<i>I. graduacauda</i>	12	4.75	7.25	0
<i>I. gularis</i>	0	7.25	4.75	0
<i>I. parisorum</i>	12	4	8	0
<i>I. spurius</i>	12	0	12	0
<i>Junco</i> (2)	4.8	.13	10.25	1.63
<i>J. hyemalis</i>	5.6	.25	9.5	2.25
<i>J. phaeonotus</i>	4	0	11	1
<i>Leucosticte</i> (1)	4	2	10	0
<i>L. arctoa</i>	4	2	10	0
<i>Melospiza</i> (3)	0	0	10	2
<i>M. georgiana</i>	0	0	10.5	1.5
<i>M. lincolnii</i>	0	0	10	2
<i>M. melodia</i>	0	0	9.5	2.5
<i>Myioborus</i> (1)	0	1.5	9.5	1
<i>M. pictus</i>	0	1.5	9.5	1
<i>Passer</i> (2)	3	0	11.5	.5
<i>P. domesticus</i>	6	0	11.5	.5
<i>P. montanus</i>	0	0	11.5	.5
<i>Pheucticus</i> (2)	10	2.35	6.95	2.7
<i>P. ludovicianus</i>	10	1.2	7.4	3.4
<i>P. melanocephalus</i>	10	3.5	6.5	2
<i>Pinicola</i> (1)	9	8.5	3.5	0
<i>P. enucleator</i>	9	8.5	3.5	0



TABLE 1 (Continued)

ANALYSIS GROUP	GENERIC AVERAGES AND SPECIES VALUES			
	Dichromatism	Carotenoid	Melanin	Structural
<i>Piranga</i> (4)	12	9.81	2.19	0
<i>P. flava</i>	12	8.5	3.5	0
<i>P. ludoviciana</i>	12	9.25	2.75	0
<i>P. olivacea</i>	12	10	2	0
<i>P. rubra</i>	12	11.5	.5	0
<i>Poecetes</i> (1)	0	0	9	3
<i>P. gramineus</i>	0	0	9	3
<i>Protonotaria</i> (1)	7	7	1	4
<i>P. citrea</i>	7	7	1	4
<i>Spizella</i> (6)	.33	0	10.5	1.5
<i>S. arborea</i>	0	0	12	0
<i>S. atrogularis</i>	2	0	11	1
<i>S. breweri</i>	0	0	9	3
<i>S. pallida</i>	0	0	9	3
<i>S. passerina</i>	0	0	10	2
<i>S. pusilla</i>	0	0	12	0
<i>Vermivora</i> (10)	3.6	2.6	6.8	2.6
<i>V. bachmanii</i>	4	3.5	7.5	1
<i>V. celata celata</i>	1	1.5	7.5	3
<i>V. celata lutescens</i>	7	5.5	6	.5
<i>V. chrysoptera</i>	4	1	6.5	4.5
<i>V. crissalis</i>	0	0	12	0
<i>V. luciae</i>	2	2	6	4
<i>V. peregrina</i>	5	0	5.5	6.5
<i>V. pinus</i>	5	6	2	4
<i>V. ruficapilla</i>	6	4	7.5	.5
<i>V. virginiae</i>	2	2.5	7.5	2
Sylvoidea:				
<i>Auriparus</i> (1)	5	4	8	0
<i>A. flaviceps</i>	5	4	8	0
<i>Campylorhynchus</i> (1)	0	0	7	5
<i>C. brunneicapillus</i>	0	0	7	5
<i>Certhia</i> (1)	0	0	7	5
<i>C. americana</i>	0	0	7	5
<i>Chamaea</i> (1)	0	0	12	0
<i>C. fasciata</i>	0	0	12	0
<i>Hirundo</i> (3)	4	0	5	7
<i>H. fulva</i>	0	0	6	6
<i>H. pyrrhonota</i>	0	0	5	7
<i>H. rustica</i>	12	0	4	8
<i>Parus</i> (9)	0	0	10.22	1.78
<i>P. atricapillus</i>	0	0	10	2
<i>P. bicolor</i>	0	0	8.5	3.5
<i>P. carolinensis</i>	0	0	10	2
<i>P. gambeli</i>	0	0	10	2
<i>P. hudsonicus</i>	0	0	10	2
<i>P. inornatus</i>	0	0	12	0
<i>P. rufescens</i>	0	0	9.5	2.5
<i>P. sclateri</i>	0	0	11	1
<i>P. wollweberi</i>	0	0	11	1
<i>Polioptila</i> (3)	3.67	0	5.67	6.33
<i>P. caerulea</i>	3	0	.5	11.5
<i>P. melanura</i>	3	0	9	3
<i>P. nigriceps</i>	5	0	7.5	4.5

TABLE 1 (Continued)

ANALYSIS GROUP	GENERIC AVERAGES AND SPECIES VALUES			
	Dichromatism	Carotenoid	Melanin	Structural
<i>Progne</i> (1)	4	0	7	5
<i>P. subis</i>	4	0	7	5
<i>Psaltiriparus</i> (1)	1	0	11	1
<i>P. minimus</i>	1	0	11	1
<i>Regulus</i> (2)	1	.5	9	2.5
<i>R. calendula</i>	1	.5	11.5	0
<i>R. satrapa</i>	1	.5	6.5	5
<i>Riparia</i> (1)	0	0	9	3
<i>R. riparia</i>	0	0	9	3
<i>Sitta</i> (4)	1.5	1.13	7.88	3
<i>S. canadensis</i>	4	3.5	7	1.5
<i>S. carolinensis</i>	2	1	6.5	4.5
<i>S. pusilla</i>	0	0	9	3
<i>S. pygmaea</i>	0	0	9	3
<i>Stelgidopteryx</i> (1)	0	0	8	4
<i>S. serripennis</i>	0	0	8	4
<i>Thryomanes</i> (1)	0	0	8	4
<i>T. bewickii</i>	0	0	8	4
<i>Thryothorus</i> (1)	0	0	9	3
<i>T. ludovicianus</i>	0	0	9	3
<i>Troglodytes</i> (2)	0	0	12	0
<i>T. aedon</i>	0	0	12	0
<i>T. troglodytes</i>	0	0	12	0
Tyrannidae:				
<i>Camptostoma</i> (1)	0	0	10	2
<i>C. imberbe</i>	0	0	10	2
<i>Contopus</i> (4)	0	0	10	2
<i>C. borealis</i>	0	0	9.5	2.5
<i>C. pertinax</i>	0	0	11	1
<i>C. sordidulus</i>	0	0	9.5	2.5
<i>C. virens</i>	0	0	10	2
<i>Empidonax</i> (10)	0	.4	9.1	2.5
<i>E. alnorum</i>	0	.5	8.5	3
<i>E. difficilis</i>	0	.5	9.5	2
<i>E. flaviventris</i>	0	.5	8.5	3
<i>E. fulvifrons</i>	0	0	10	2
<i>E. hammondii</i>	0	.5	10.5	1
<i>E. minimus</i>	0	.5	9.5	2
<i>E. oberholseri</i>	0	.5	9.5	2
<i>E. traillii</i>	0	.5	9.5	2
<i>E. virens</i>	0	.5	6.5	5
<i>E. wrightii</i>	0	0	9	3
<i>Myiarchus</i> (4)	0	1.25	10	.75
<i>M. cinerascens</i>	0	1	10	1
<i>M. crinitus</i>	0	2	10	0
<i>M. tuberculifer</i>	0	1	10	1
<i>M. tyrannulus</i>	0	1	10	1
<i>Myiodynastes</i> (1)	0	1.5	7.25	3.25
<i>M. luteiventris</i>	0	1.5	7.25	3.25
<i>Pachyramphus</i> (1)	10	1	11	0
<i>P. aglaiae</i>	10	1	11	0
<i>Pitangus</i> (1)	0	3.5	6.5	2
<i>P. sulphuratus</i>	0	3.5	6.5	2
<i>Pyrocephalus</i> (1)	12	6	6	0
<i>P. rubinus</i>	12	6	6	0

TABLE 1 (Continued)

ANALYSIS GROUP	GENERIC AVERAGES AND SPECIES VALUES			
	Dichromatism	Carotenoid	Melanin	Structural
<i>Sayornis</i> (3)	0	0	10.33	1.67
<i>S. nigricans</i>	0	0	10	2
<i>S. phoebe</i>	0	0	9	3
<i>S. saya</i>	0	0	12	0
<i>Tyrannus</i> (8)	.38	1.81	8.25	1.94
<i>T. couchii</i>	0	2.5	7.5	2
<i>T. crassirostris</i>	0	.5	8.5	3
<i>T. dominicensis</i>	0	.5	8.5	3
<i>T. forficatus</i>	3	3	8.5	.5
<i>T. melancholicus</i>	0	2.5	7.5	2
<i>T. tyrannus</i>	0	.5	7.5	4
<i>T. verticalis</i>	0	2.5	9	.5
<i>T. vociferans</i>	0	2.5	9	.5

NOTE.—Values in parentheses give the number of species averaged. The generic averages were converted to proportions, and the arcsine of the square root of the proportion was used in the analysis.

various evolutionary assumptions. The comparison of observed and expected correlations is made via a *Z* score. Simulations were performed by the PDSIMUL module of the Phenotypic Diversity Analysis Program (Garland et al. 1993). The simulation “evolves” the traits up the given phylogeny by drawing changes from a bivariate normal probability distribution set to have a mean change of zero and an intertrait correlation of zero for each analysis. The variance of the distribution was set such that the variance of the tip values of the simulated data would be similar to that of the real data for Brownian motion simulations. However, because the data consist of transformed proportions, the simulations were bounded such that the traits could not evolve either below zero or above 1.5708 (i.e., the arcsine of the square root of zero and one, respectively). If a change was drawn during a simulation that would result in the traits exceeding these bounds, that change was discarded and replaced by another randomly selected change (see Garland et al. 1993).

Different simulation models were used to incorporate different models of evolutionary change. Evolution by random genetic drift both with and without stabilizing selection was modeled. Random genetic drift without stabilizing selection was modeled as a Brownian motion process in which successive changes were independent of each other and of the starting value. Stabilizing selection may be a more realistic model for many traits, including sexually selected ones. Sexually selected traits are often viewed as stabilized by the counteracting forces of directional sexual selection for greater trait expression and directional natural selection for lesser trait expression. Stabilizing selection was modeled as a Brownian motion process with the addition of a linear force that tends to return the traits toward an adaptive peak (Felsenstein 1988; Garland et al. 1993). These are referred to as Ornstein-Uhlenbeck models. The strength of stabilizing selection can

range from nonexistent to infinitely strong. I modeled both fairly weak and fairly strong stabilizing selection. The stabilizing selection parameters were equal to the inverse of the total tree height for weak stabilizing selection and 10 times this for strong stabilizing selection (for discussion, see Garland et al. 1993 and the PDSIMUL documentation). The values for the adaptive peaks were set equal to the clades' starting trait values (i.e., the mean of the tip values) and were assumed not to change.

Both gradual change and speciation change were modeled for all of these methods (i.e., for both independent contrasts and computer simulations). Under gradual models, the expected amount of change on a branch is proportional to the length of that branch; for speciation change, all branches are set to equal length. The independent contrasts from speciation models may not prove to be adequately standardized. Transformations, however, would nullify the assumption of the speciation model. Therefore, even when contrasts from the speciation independent contrasts methods were not adequately standardized, the branch lengths were not transformed (i.e., the speciation assumption was retained). In these instances, the resulting correlations are less trustworthy, as all data points may not receive equal weight.

Combining the different analysis methods and their evolutionary assumptions gives a total of eight different methods for testing the correlated evolution of color origin and sexual dichromatism. These are as follows: gradual and speciation independent contrasts, gradual and speciation Brownian motion simulations, and gradual and speciation Ornstein-Uhlenbeck simulations with both weak and strong stabilizing selection. Together these methods incorporate a rather wide range of evolutionary scenarios.

Analyses were performed on the entire clade of passerines and were performed separately for the subclades Tyrannidae, Corvoidea, Sylvioidea, Muscipoidea, and Passeroidea as defined in Sibley and Ahlquist (1990). Only genera with phylogenetic information in Sibley and Ahlquist (1990, pp. 855–870) were used; genera for which no data were available were deleted from the phylogeny. The difference in  $\Delta T_{50H}$  values between two nodes (or a node and a tip) was used for the length of the branch connecting the nodes. Separate analyses were performed for carotenoid, melanin, and structural colors. One-tailed  $P$  values are reported for the correlation between dichromatism and carotenoids; two-tailed  $P$  values are reported for the correlations between dichromatism and melanin and dichromatism and structurally derived colors. One-tailed  $P$  values are preferred for the carotenoid analyses, as the a priori hypothesis is explicitly directional, predicting positive correlations.

## RESULTS

### *Independent Contrasts Methods*

The results of the independent contrasts methods are given in table 2 and figures 1–3. In passerines as a whole, no branch length transformations were found to be necessary ( $P > .05$  for all correlations of contrasts with their standard

TABLE 2  
RESULTS OF INDEPENDENT CONTRASTS METHODS

	CAROTENOID		MELANIN		STRUCTURAL	
	<i>r</i>	df	<i>r</i>	df	<i>r</i>	df
All passerines:						
Gradual	.340	66-70**	-.267	66-70†	-.048	66-70 (NS)
Speciational	.359	66**, 67-70***	-.287	66-70†	-.050	66-70 (NS)
Tyrannidae:						
Gradual	.645	6-8*	-.354	6-8 (NS)	-.833	6-8††
Speciational	.803	6-8**	-.401	6-8 (NS)	-.857	6-8††
Corvoidea:						
Gradual	.105	6-8 (NS)	-.024	6-8 (NS)	.020	6-8 (NS)
Speciational	.276	6-8 (NS)	.276	6-8 (NS)	-.300	6-8 (NS)
Sylvioidea:						
Gradual	.329	14 (NS)	-.427	14 (NS)	.217	14 (NS)
Speciational	.431	14*	-.364	14 (NS)	.115	14 (NS)
Muscicapoidea:						
Gradual	-.233	11 (NS)	.102	11 (NS)	-.082	11 (NS)
Speciational	-.397	11 (NS)	-.392	11 (NS)	.460	11 (NS)
Passeroidea:						
Gradual	.461	21*	-.357	21 (NS)	-.223	21 (NS)
Speciational	.487	21**	-.383	21 (NS)	-.252	21 (NS)

NOTE.—The correlation of independent contrasts is indicated by *r*. The degrees of freedom encompass a range for some groups. This is a result of polytomies (see text).

\*  $P < .05$ , one-tailed test.

\*\*  $P < .01$ , one-tailed test.

\*\*\*  $P < .001$ , one-tailed test.

†  $P < .05$ , two-tailed test.

††  $P < .01$ , two-tailed test.

deviations) for tests assuming gradual change. For speciation tests, the dichromatism contrasts were not adequately standardized (correlation between the absolute value of the standardized contrasts and their standard deviations:  $r = 0.282$ ,  $df = 65-69$ ,  $P < .05$ ). Assuming gradual evolution, changes in carotenoid coloration correlate positively with changes in dichromatism ( $r = 0.340$ ,  $df = 66-70$ ,  $P < .01$ ). Changes in melanins correlate negatively with changes in dichromatism ( $r = -0.267$ ,  $df = 66-70$ ,  $P < .05$ ). Changes in structural coloration do not correlate significantly with changes in dichromatism ( $r = -0.048$ ,  $df = 66-70$ ,  $P > .05$ ). Despite the poor standardization of the dichromatism contrasts, the results of the speciation model are qualitatively identical (carotenoids:  $r = 0.359$ ,  $P < .01$ ; melanins:  $r = -0.287$ ,  $P < .05$ ; structurals:  $r = -0.050$ ,  $P > .05$ ;  $df = 66-70$ ).

In the Tyrannidae, contrasts were adequately standardized both for the gradual and for the speciation model ( $P > .05$  for all comparisons). Changes in carotenoid coloration correlate positively with changes in dichromatism (gradual model:  $r = 0.645$ ,  $P < .05$ ,  $df = 6-8$ ; speciation model:  $r = 0.803$ ,  $P < .01$ ,  $df = 6-8$ ). Changes in melanin coloration do not correlate significantly with changes in dichromatism (gradual model:  $r = -0.354$ ,  $P > .05$ ,  $df = 6-8$ ; specia-

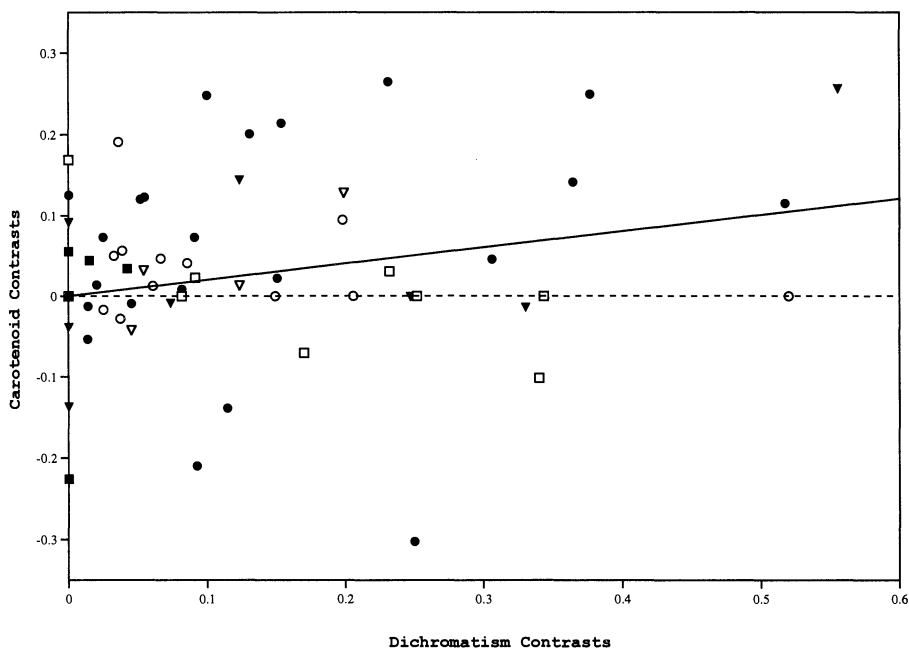


FIG. 1.—The relationship between standardized independent contrasts of carotenoid coloration and dichromatism. Thirteen points overlap at the origin (0,0); all others are shown, although several are partially obscured. Plotting symbols indicate contrasts within subclades: filled and open squares represent contrasts within the Corvoidea and the Muscipoidea, respectively; filled and open circles represent contrasts within the Passeroidea and the Sylvioidea, respectively; filled and open triangles represent contrasts within the Tyrannidae and basal contrasts among the five subclades, respectively.

tional model:  $r = -0.401$ ,  $P > .05$ ,  $df = 6-8$ ). Changes in structural coloration correlate negatively with changes in dichromatism (gradual model:  $r = -0.833$ ,  $P < .01$ ,  $df = 6-8$ ; speciation model:  $r = -0.857$ ,  $P < .01$ ,  $df = 6-8$ ).

In the Corvoidea, contrasts were not adequately standardized for the gradual model (dichromatism contrasts:  $r = 0.727$ ; melanin contrasts:  $r = -0.711$ ; structural contrasts:  $r = -0.674$ ,  $df = 5-7$ ,  $P < .05$ ) or for the speciation model (dichromatism contrasts:  $r = 0.675$ ,  $df = 5-7$ ,  $P < .05$ ). For the gradual model, branch lengths were transformed by raising them to the fourth power and then rescaling the total tree height back to the original total height. This resulted in adequate standardization for all traits. No significant correlations between changes in coloration and changes in dichromatism were found (gradual model: carotenoid  $r = 0.105$ , melanin  $r = -0.024$ , structural  $r = 0.020$ ; speciation model: carotenoid  $r = 0.276$ , melanin  $r = 0.276$ , structural  $r = -0.300$ ;  $df = 6-8$ ,  $P > .05$  for all tests).

In the Sylvioidea, dichromatism contrasts were not adequately standardized for the gradual model ( $r = -0.532$ ,  $df = 13$ ,  $P < .05$ ). Contrasts were adequately

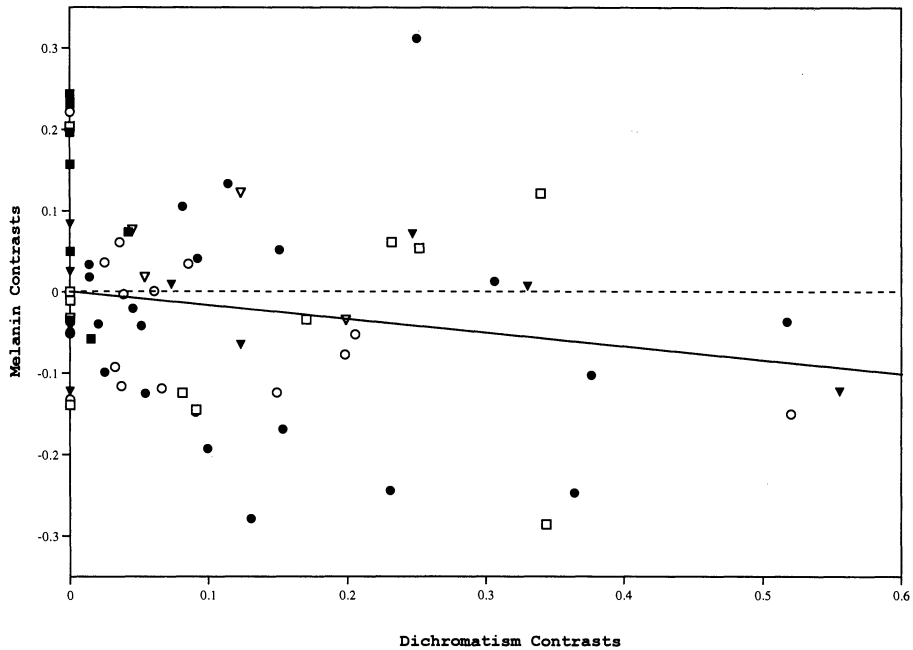


FIG. 2.—The relationship between standardized independent contrasts of melanin coloration and dichromatism. All points are shown, although several are partially obscured. Plotting symbols are as in figure 1.

standardized for all traits in the speciational model. For the gradual model, branch lengths were square-root transformed. This resulted in adequate standardization of contrasts for all traits. Changes in carotenoids correlate positively with changes in dichromatism for the speciational, but not the gradual model (gradual model:  $r = 0.329$ ,  $df = 14$ ,  $P > .05$ ; speciational model:  $r = 0.431$ ,  $df = 14$ ,  $P < .05$ ). No significant results were found for either melanin or structural colors (gradual model: melanin  $r = -0.427$ , structural  $r = 0.217$ ; speciational model: melanin  $r = -0.364$ , structural  $r = 0.115$ ;  $df = 14$ ,  $P > .05$  for all tests).

In the Muscipoidea, dichromatism contrasts were not adequately standardized for the gradual model ( $r = 0.645$ ,  $df = 10$ ,  $P < .05$ ). Contrasts were adequately standardized for all traits in the speciational model. For the gradual model, branch lengths were transformed by raising them to the fourth power and then rescaling the total tree height back to the original total height. This resulted in adequate standardization for all traits. No significant correlations between changes in coloration and changes in dichromatism were found (gradual model: carotenoid  $r = -0.233$ , melanin  $r = 0.102$ , structural  $r = -0.082$ ; speciational model: carotenoid  $r = -0.397$ , melanin  $r = -0.392$ , structural  $r = 0.460$ ;  $df = 11$ ,  $P > .05$  for all tests).

In the Passeroidea, dichromatism contrasts were not adequately standardized

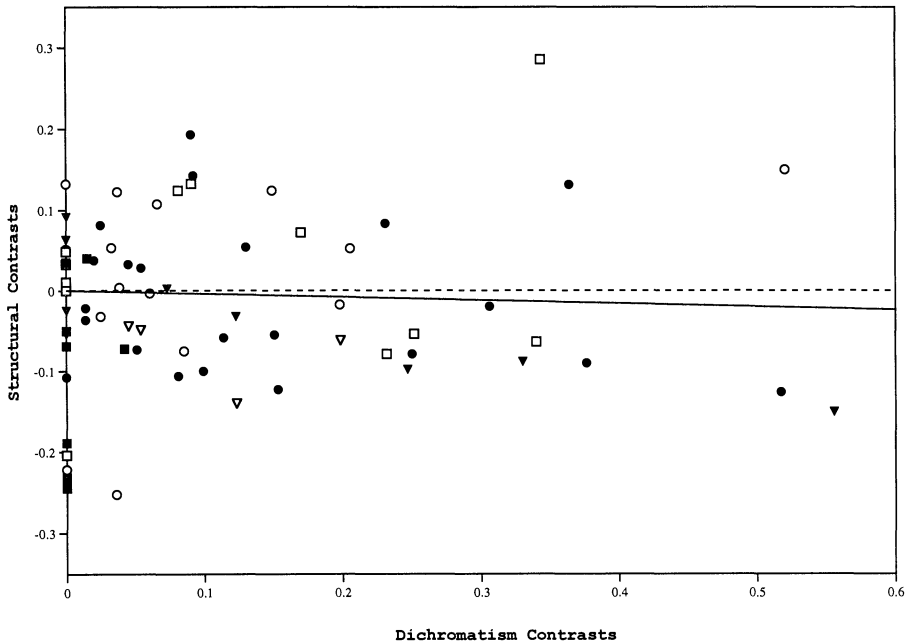


FIG. 3.—The relationship between standardized independent contrasts of structural coloration and dichromatism. Two points overlap on the Y-axis (0, -0.24); all other points are shown, although several are partially obscured. Plotting symbols are as in figure 1.

for the gradual model ( $r = -0.427$ ,  $df = 20$ ,  $P < .05$ ). For the speciation model, carotenoid contrasts were not adequately standardized ( $r = 0.440$ ,  $df = 20$ ,  $P < .05$ ). For the gradual model, branch lengths were square-root transformed. This resulted in adequate standardization of contrasts for all traits. Changes in carotenoids correlate positively with changes in dichromatism (gradual model:  $r = 0.461$ ; speciation model:  $r = 0.487$ ;  $df = 21$ ,  $P < .05$  gradual model,  $P < .01$  speciation model). No significant results were found for either melanin or structural colors (gradual model: melanin  $r = -0.357$ , structural  $r = -0.223$ ; speciation model: melanin  $r = -0.383$ , structural  $r = -0.252$ ;  $df = 21$ ,  $P > .05$  for all tests).

#### Simulation Methods

The results of the simulation methods are presented in table 3. The passerines as a whole show a positive Pearson product-moment correlation between carotenoids and dichromatism ( $r = 0.524$ ,  $P < .05$  for all analysis methods). Furthermore, all five subclades show positive correlations between carotenoids and dichromatism (binomial sign test,  $P < .05$ ). No significant association between melanins and dichromatism was found in passerines as a whole ( $r = -0.208$ ,  $P > .05$  for all analysis methods). However, all five subclades show a negative



TABLE 3  
RESULTS OF COMPUTER SIMULATION METHODS

Analysis Group and Method	Mean (SD)	Z Score
All passerines (number of tips = 72):		
Carotenoid ( $r = .524$ ):		
GB	-.003 (.198)	2.662**
SB	.033 (.213)	2.305*
GOUW	.013 (.162)	3.154***
GOUS	-.003 (.123)	4.285***
SOUW	.010 (.171)	3.006**
SOUS	.001 (.122)	4.287***
Melanin ( $r = -.208$ ):		
GB	.008 (.203)	-1.064 (NS)
SB	.000 (.231)	-.900 (NS)
GOUW	.013 (.171)	-1.292 (NS)
GOUS	.003 (.130)	-1.623 (NS)
SOUW	-.003 (.204)	-1.005 (NS)
SOUS	.001 (.122)	-1.713 (NS)
Structural ( $r = -.285$ ):		
GB	-.002 (.203)	-1.394 (NS)
SB	.023 (.222)	-1.387 (NS)
GOUW	.004 (.162)	-1.784 (NS)
GOUS	.003 (.130)	-2.215†
SOUW	-.003 (.204)	-1.382 (NS)
SOUS	.001 (.122)	-2.344†
Tyrannidae (number of tips = 10):		
Carotenoid ( $r = .591$ ):		
GB	.000 (.354)	1.670*
SB	.058 (.359)	1.485 (NS)
GOUW	.022 (.355)	1.603 (NS)
GOUS	.005 (.347)	1.689*
SOUW	-.001 (.359)	1.649*
SOUS	-.015 (.328)	1.848*
Melanin ( $r = -.177$ ):		
GB	.001 (.367)	-.485 (NS)
SB	-.009 (.382)	-.440 (NS)
GOUW	.006 (.352)	-.486 (NS)
GOUS	.005 (.347)	-.525 (NS)
SOUW	-.001 (.359)	-.490 (NS)
SOUS	-.015 (.328)	-.494 (NS)
Structural ( $r = -.905$ ):		
GB	.001 (.372)	-2.436†
SB	.023 (.359)	-2.585††
GOUW	.002 (.340)	-2.668††
GOUS	.005 (.347)	-2.623††
SOUW	-.001 (.359)	-2.518†
SOUS	-.015 (.328)	-2.713††
Corvoidea (number of tips = 10):		
Carotenoid ( $r = .298$ ):		
GB	-.002 (.355)	.845 (NS)
SB	.134 (.360)	.456 (NS)
GOUW	.034 (.341)	.774 (NS)
GOUS	.007 (.337)	.864 (NS)
SOUW	.043 (.349)	.731 (NS)
SOUS	-.006 (.344)	.884 (NS)

TABLE 3 (Continued)

Analysis Group and Method	Mean (SD)	Z Score
Melanin ( $r = -.041$ ):		
GB	.010 (.365)	-.140 (NS)
SB	.000 (.378)	-.109 (NS)
GOUW	.002 (.342)	-.126 (NS)
GOUS	.007 (.355)	-.135 (NS)
SOUW	.003 (.344)	-.128 (NS)
SOUS	-.006 (.344)	-.102 (NS)
Structural ( $r = -.066$ ):		
GB	-.007 (.356)	-.166 (NS)
SB	-.011 (.379)	-.145 (NS)
GOUW	-.001 (.345)	-.188 (NS)
GOUS	.007 (.355)	-.206 (NS)
SOUW	.003 (.349)	-.198 (NS)
SOUS	-.006 (.344)	-.174 (NS)
Sylvioidea (number of tips = 16):		
Carotenoid ( $r = .508$ ):		
GB	.003 (.290)	1.741*
SB	.046 (.317)	1.457 (NS)
GOUW	.014 (.275)	1.796*
GOUS	-.004 (.283)	1.809*
SOUW	.007 (.274)	1.829*
SOUS	-.005 (.254)	2.020*
Melanin ( $r = -.457$ ):		
GB	.005 (.305)	-1.515 (NS)
SB	.013 (.355)	-1.324 (NS)
GOUW	.003 (.286)	-1.608 (NS)
GOUS	-.005 (.286)	-1.580 (NS)
SOUW	.017 (.301)	-1.575 (NS)
SOUS	-.005 (.254)	-1.780 (NS)
Structural ( $r = .153$ ):		
GB	.010 (.308)	.464 (NS)
SB	.016 (.341)	.402 (NS)
GOUW	.007 (.282)	.518 (NS)
GOUS	-.005 (.286)	.552 (NS)
SOUW	.008 (.307)	.472 (NS)
SOUS	-.005 (.254)	.622 (NS)
Muscicapoidea (number of tips = 13):		
Carotenoid ( $r = .076$ ):		
GB	.002 (.322)	.230 (NS)
SB	.059 (.328)	.052 (NS)
GOUW	-.012 (.310)	.284 (NS)
GOUS	-.005 (.306)	.265 (NS)
SOUW	.007 (.304)	.227 (NS)
SOUS	.012 (.288)	.222 (NS)
Melanin ( $r = -.272$ ):		
GB	-.001 (.329)	-.824 (NS)
SB	-.046 (.343)	-.659 (NS)
GOUW	.007 (.305)	-.915 (NS)
GOUS	-.004 (.307)	-.873 (NS)
SOUW	.003 (.313)	-.879 (NS)
SOUS	-.001 (.285)	-.951 (NS)

TABLE 3 (Continued)

Analysis Group and Method	Mean (SD)	Z Score
Structural ( $r = .258$ ):		
GB	.010 (.327)	.758 (NS)
SB	.022 (.334)	.707 (NS)
GOUW	.011 (.305)	.810 (NS)
GOUS	-.004 (.307)	.853 (NS)
SOUW	.019 (.303)	.789 (NS)
SOUS	-.001 (.285)	.909 (NS)
Passeroidea (number of tips = 23):		
Carotenoid ( $r = .537$ ):		
GB	.001 (.247)	2.170*
SB	.012 (.279)	1.882*
GOUW	.016 (.238)	2.189*
GOUS	.005 (.217)	2.452**
SOUW	.013 (.259)	2.023*
SOUS	.003 (.208)	2.567**
Melanin ( $r = -.299$ ):		
GB	.007 (.261)	-1.172 (NS)
SB	.005 (.285)	-1.067 (NS)
GOUW	.002 (.243)	-1.239 (NS)
GOUS	.005 (.217)	-1.401 (NS)
SOUW	.003 (.272)	-1.110 (NS)
SOUS	.003 (.208)	-1.452 (NS)
Structural ( $r = -.497$ ):		
GB	.004 (.253)	-1.980†
SB	-.004 (.283)	-1.742 (NS)
GOUW	.005 (.236)	-2.127†
GOUS	.005 (.217)	-2.313†
SOUW	.012 (.268)	-1.899 (NS)
SOUS	.003 (.208)	-2.404†

NOTE.—The observed Pearson product-moment correlation between coloration and sexual dichromatism ( $r$ ) and the mean (SD) of 1,000 simulations are shown. Methods: GB, gradual Brownian motion; SB, speciation Brownian motion; GOUW, gradual Ornstein-Uhlenbeck weak; GOUS, gradual Ornstein-Uhlenbeck strong; SOUW, speciation Ornstein-Uhlenbeck weak; SOUS, speciation Ornstein-Uhlenbeck strong; all simulations were bounded (see text).

\*  $P < .05$ , one-tailed test.

\*\*  $P < .01$ , one-tailed test.

\*\*\*  $P < .001$ , one-tailed test.

†  $P < .05$ , two-tailed test.

††  $P < .01$ , two-tailed test.

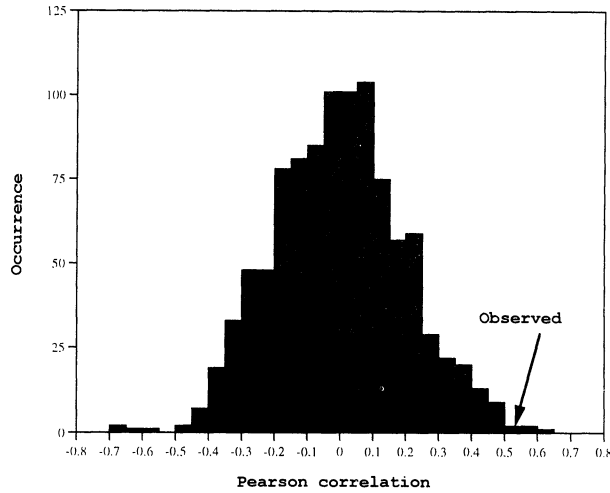


FIG. 4.—The observed correlation between the tip values of carotenoid-derived coloration and dichromatism, and the distribution of correlations of tip values of data simulated under the gradual Brownian motion model.

relationship (binomial sign test,  $P < .05$ ). Structural coloration is negatively correlated with dichromatism in passerines as a whole ( $r = -0.285$ ,  $P < .05$  for two analysis methods,  $P > .05$  for four analysis methods). The two analysis methods yielding significant results both assume fairly strong stabilizing selection on plumage coloration. In three of the five subclades, structural colors are negatively correlated with dichromatism (binomial sign test,  $P > .05$ ). Figures 4–6 show the observed tip correlation and the distribution of the correlations of the simulated tip data for passerines as a whole, assuming gradual Brownian motion.

In the Tyrannidae, carotenoids correlate positively with dichromatism ( $r = 0.591$ ,  $P < .05$ ) for four analysis methods. Neither the speciation Brownian motion nor the weak gradual Ornstein-Uhlenbeck methods give significant results. Melanins show a weak, nonsignificant negative correlation ( $r = -0.177$ ,  $P > .05$  for all methods). Structural coloration is strongly negatively correlated with dichromatism ( $r = -0.905$ ,  $P < .05$  for all methods).

In the Corvoidea, no significant relationships were found (carotenoids:  $r = 0.298$ ,  $P > .05$  for all methods; melanins:  $r = -0.041$ ,  $P > .05$  for all methods; structurals:  $r = -0.066$ ,  $P > .05$  for all methods).

In the Sylvioidea, carotenoids correlate positively with dichromatism ( $r = 0.508$ ,  $P < .05$  for all methods except speciation Brownian motion, where  $P > .05$ ). Neither melanins nor structural colors significantly correlate with dichromatism (melanins:  $r = -0.457$ ,  $P > .05$  for all methods; structurals:  $r = 0.153$ ,  $P > .05$  for all methods).

In the Muscipoidea, no significant relationships were found (carotenoids:  $r = 0.076$ ,  $P > .05$  for all methods; melanins:  $r = -0.272$ ,  $P > .05$  for all methods; structurals:  $r = 0.258$ ,  $P > .05$  for all methods).

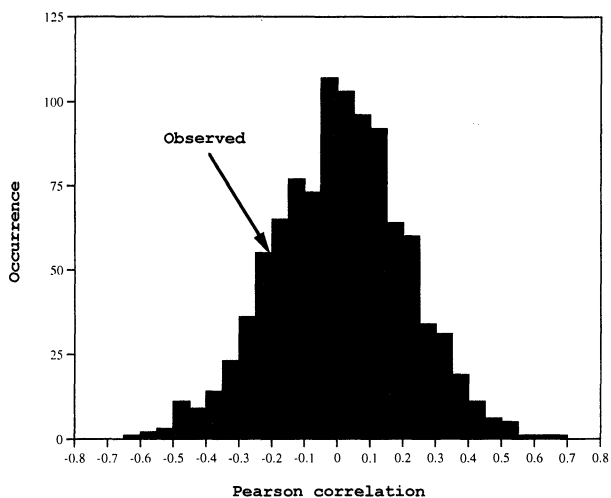


FIG. 5.—The observed correlation between the tip values of melanin-derived coloration and dichromatism, and the distribution of correlations of tip values of data simulated under the gradual Brownian motion model.

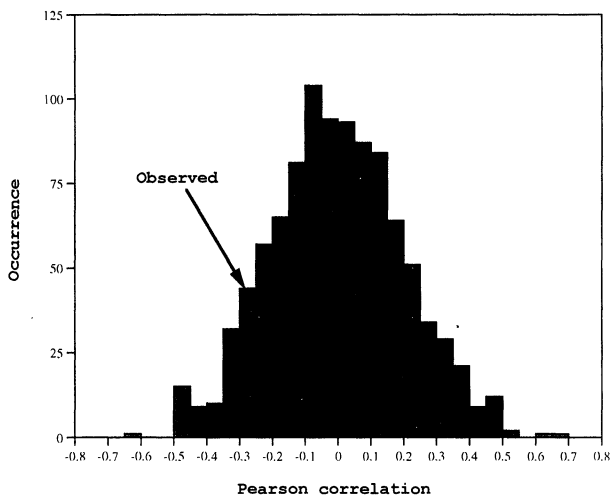


FIG. 6.—The observed correlation between the tip values of structurally derived coloration and dichromatism, and the distribution of correlations of tip values of data simulated under the gradual Brownian motion model.

In the Passeroidea, carotenoids correlate positively with dichromatism ( $r = 0.537$ ,  $P < .05$  for all methods). Melanins do not correlate significantly with dichromatism ( $r = -0.299$ ,  $P > .05$  for all methods). Structural colors negatively correlate with dichromatism ( $r = -0.497$ ,  $P < .05$  for four methods,  $P > .05$  for both the speciation Brownian motion and the weak speciation Ornstein-Uhlenbeck methods).

#### DISCUSSION

The results for passerines as a whole are supportive of the hypothesis that carotenoids should correlate positively with sexual dichromatism, whereas melanin and structurally produced colors may not. This observed pattern is attributable to three of the five subclades, although all five subclades show positive correlations (for the simulation methods). It is not at all surprising that no significant results were found in the Corvoidea, as only one genus shows any sexual dichromatism. The results for the Muscipoidea are more surprising. It is difficult to interpret these results because they depend somewhat on the analysis method used and are not statistically significant. Overall, the increase in carotenoids has been at the expense of both melanins and structural coloration. In the Tyrannidae and the Passeroidea, it appears that carotenoids have replaced mainly structural coloration. However, for passerines as a whole, the independent contrasts methods suggest that melanins have been replaced, and the simulation methods suggest (weakly) that structural colors have been replaced. The carotenoid results, combined with the generally negative correlations for both melanin and structurally derived coloration, suggest that sexual selection has favored carotenoid coloration. Clearly this does not prove that sexual selection has operated on the basis of a condition-dependent honest indicator of quality; however, one major prediction of the carotenoids-as-honest-signals hypothesis is supported.

For carotenoids to be honest signals, carotenoids should be in some way limiting. Whether or not carotenoids are limited in the wild is a matter of some debate (Hill 1994a; Hudon 1994). To date, very few empirical studies have addressed this issue. Several studies of passerine birds have shown that the degree of carotenoid ornamentation is associated with differences in dietary intake or environmental availability of carotenoids (Slagsvold and Lifjeld 1985; Partali et al. 1987; Hill and Montgomerie 1994; Hill et al. 1994; Ryan et al. 1994). For a carotenoid signaling system to be honest, carotenoids need to be available but not superabundant within the normal diet. Insectivorous and granivorous species are more likely to meet these requirements than are largely carnivorous or frugivorous species. Carnivorous species may not acquire sufficient excess carotenoids for a signaling function to evolve, whereas frugivorous species may easily acquire such large quantities of carotenoids that they may no longer be indicative of health or foraging or competitive abilities.

Carotenoids can become limiting for reasons other than environmental availability. If physiological condition affects foraging, then ornamental carotenoids have the potential to reflect physiological condition, such as disease status prior

to the last molt. Disease can also directly affect carotenoids. In fact, various parasites have been shown to decrease carotenoid pigmentation of infected hosts. The amount of carotenoid coloration in three-spined sticklebacks, *Gasterosteus aculeatus*, has been shown to correlate positively with male condition and freedom from parasites (Milinski and Bakker 1990). The red eye coloration of red jungle fowl, *Gallus gallus*, which is partially carotenoid based, is negatively affected by an intestinal parasite (Zuk et al. 1990a). In domestic fowl, carotenoid levels are negatively affected by infection with coccidia (Ruff et al. 1974). The carotenoid spots of guppies, *Poecilia reticulata*, are negatively affected by at least one type of parasitic infection (Houde and Torio 1992). Disease states are associated with reduced carotenoid activity in humans. Intestinal parasites, liver, kidney, and thyroid diseases, and systemic infections and stress reduce circulating levels of vitamin A or its derivatives (reviewed in Underwood 1984).

Carotenoids are the essential vitamin A precursors (Pitt 1971; Underwood 1984). Vitamin A and its derivatives are involved in growth, vision, cell differentiation, spermatogenesis, and immune function (Dennert 1984; Moon and Itri 1984; Roberts and Sporn 1984; Underwood 1984; Mather and Phillips 1986). This has two important implications. First, display carotenoids should be in excess of those required physiologically. Discussions of whether or not carotenoids are limiting must include baseline physiological levels as well as ornamental requirements. Second, we should not expect that the mechanisms of carotenoid manipulation, storage, and deposition are maximized solely for display purposes. If carotenoids are, or periodically become, limiting, then individuals should maintain biochemical pathways that reserve carotenoids for physiological use, rather than exclusively maximize display independent of physiological requirements. Absolute maximization of sexual display, at the expense of maintenance, is probably very rare in iteroparous species.

Phylogenetic analyses are explicitly historical. Correlated changes in traits imply past selection, or genetic correlation and covariance (Leroi et al. 1994); the results need not imply current selection for carotenoids in sexually dichromatic species. Nonetheless, examples of current selection can provide additional support for the hypothesis. Before assessing these examples, it is important to emphasize that the results would be predicted independently of whether male-male competition or female choice is the stronger sexually selective force. This is because it should pay both sexes to heed signals that are reliably associated with quality (Butcher and Rohwer 1989).

Current selection along the lines proposed here has been demonstrated in a few instances. In fish, female three-spined sticklebacks, *G. aculeatus*, prefer males with greater carotenoid-derived red coloration (Bakker and Mundwiler 1994). In guppies, *P. reticulata*, females prefer males with more and brighter carotenoid-derived orange spots (Endler 1983; Kodric-Brown 1985, 1989). In birds, female house finches, *Carpodacus mexicanus*, prefer males with more carotenoid-derived red plumage (Hill 1990, 1991, 1994b). In American goldfinches, *Carduelis tristis*, females prefer males with brighter yellow plumage and orange

bill color, which are carotenoid derived (Johnson et al. 1993). The bright yellow underwing of male village weavers, *Ploceus cucullatus*, is important in attracting females to nest sites (Collias et al. 1979). The bright yellow is known to be carotenoid derived (Fox 1976). The bright red epaulets of male red-winged blackbirds, *Agelaius phoeniceus*, are important in male-male competition for territories (Peek 1972; Smith 1972; Røskoft and Rohwer 1987). On the basis of appearance, the epaulets seem likely to be carotenoid derived, but to my knowledge this has not been tested biochemically. In red jungle fowl, *G. gallus*, plumage color is caused by melanins (Witschi 1961), whereas eye color is affected by carotenoids (Fox 1976). The effects of plumage on female choice are unclear (contrast Zuk et al. 1990b with Ligon and Zwartjes 1995), although females do seem to prefer males with redder eyes (Zuk et al. 1990b).

Mating system and male parental care are not controlled for in this study. Polygynous mating systems are not invariably associated with strong sexual dimorphism. In fact, nearly 25% of avian lekking species are monomorphic (Trail 1990). The effects of early breeding and potential second clutches (Darwin 1871; Selander 1972), male-biased sex ratios (Darwin 1871; Lack 1954; Witschi 1961), possible cuckoldry via prepairing copulation (Moore and McDonald 1993), and extrapair copulations (Ford 1983; Birkhead 1987; Birkhead et al. 1988; Møller and Birkhead 1994) are argued to be sufficient to promote strong sexual selection. Parental care does not vary extensively among North American passerines (Verner and Willson 1969). In a comparative test of the Hamilton and Zuk (1982) hypothesis, Johnson (1991) found no difference in the conspicuousness of monogamous and polygynous North American passerine families or subfamilies. Among the families or subfamilies that do show variation in sex-specific incubation, no association with male plumage conspicuousness was found. Johnson's analysis is especially relevant to this study, as it reserved the maximally conspicuous plumage scores for bright reds and yellows (i.e., probable carotenoids) and blues, attempted to control for phylogeny (albeit in a manner different from this study), and analyzed North American passerines, and so consists of a sample very similar to that used here. Similarly, in a review of European passerines, Møller (1986) found that monogamous and polygynous species were equally dimorphic in plumage brightness. Thus, the effects of these potentially confounding variables are thought to be minimal or nonexistent.

The association between carotenoid-derived male plumage coloration and sexual dichromatism demonstrated here is easily incorporated into good genes or condition-dependent models of sexual selection. However, two alternate hypotheses need to be addressed. The first is the sensory-bias model of sexual selection (Basolo 1990; Ryan and Keddy-Hector 1992), in which male traits are elaborated solely because of their stimulatory effect on female perceptual or nervous systems. The sensory-bias model would argue that carotenoid-derived plumage was elaborated in males because female perceptual or nervous systems respond more strongly to colors that humans perceive as reds, yellows, and oranges. Such a female bias could be caused by either innate factors or perhaps because of an association between red, yellow, or orange stimuli and important naturally se-



lected ecological factors, for example, red berries as food sources. The Tyrannidae can serve as a good counterexample to both types of biases. Both innate and ecological biases favoring carotenoid-derived colors are unlikely in insectivorous species because of the potential danger of yellow warning-colored insects, particularly various Hymenoptera. An innate avoidance mechanism is more likely and has been demonstrated for the avoidance of coral snakes by kiskadees (Smith 1977). Despite the foregoing, it remains possible that carotenoids have been favored simply because they are bright.

The second alternative hypothesis that needs consideration is the unprofitable prey model of Baker and Parker (1979). In essence, they propose that brightness in birds evolved to signal to predators that the prey are either noxious, potentially dangerous, or simply alert and aware of the predator, any of which make the prey less valuable to the predator. Krebs (1979) and Lyon and Montgomerie (1985) argue that causation is not clearly established and that the sexual selection hypothesis is not substantially refuted by either Baker and Parker (1979) or Baker and Hounscome (1983). Experimental evidence is scarce and has yet to resolve this issue (Götmark 1993). Nonetheless, the carotenoid results presented here could be interpreted as representing honest signals whether directed by males to other males, females, or predators. The results would then be interpreted in the context of signal selection (Hasson 1990, 1991; Zahavi 1991). If this were the case, then carotenoid-derived plumage should correlate with predation risk.

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